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# THE GENETICS OF *PAPILIO DARDANUS* BROWN (LEP.)

By E. B. Ford, M.A., B.Sc.

*(Lecturer in Genetics, and University Demonstrator in the Department of Comparative Anatomy, Oxford.)*

[Read 4th March, 1936.]

With Plates 1 to 4.

Contents.

| | PAGE |
|---|---|
| 1. Introduction | 435 |
| 2. Races and Distribution | 436 |
| 3. Genetics | 444 |
| 4. The variability of subsp. *polytrophus* | 452 |
| 5. Suggestions for future research | 455 |
| 6. Tables of bred families | 458 |
| 7. Summary | 463 |
| 8. References | 464 |
| 9. Appendix | 465 |

## 1. Introduction.

*Papilio dardanus* Brown, provides one of the most remarkable instance of polymorphism to be found among the Lepidoptera. It is divided into a number of geographical races, and in nearly all of them the females exist in a variety of forms, generally mimicking such protected Danaine or Acraeine models as are available in the region they inhabit. The males, however, are everywhere monomorphic and non-mimetic. The importance of such a situation to all students of evolution need not be stressed. Furthermore, the phenomenon of polymorphism has in recent years become of special significance to geneticists, owing to the intrinsic interest of the mechanism by which it is controlled and to the valuable material it provides for the study of dominance-modification. No work on these subjects has so far been attempted in *P. dardanus*, though the species provides exceptional opportunities for it. Indeed, save for a few tentative suggestions (p. 444), the genetic relation of the different female forms is entirely unknown. Yet I have been surprised to find how great an amount of material already lies to hand. Though this is a large insect requiring considerable space and attention, and although it is one which has never yet been bred outside Africa, I have been able to obtain details of 124 bred families. Accounts of only 40 of these have been published, and in the form of scattered records which have never been brought together. Doubtless other broods exist in collections unavailable to me, but their number is not likely to be large. It is an unfortunate fact that the value of these data is much less than might at first be supposed, owing to the probability that mixed matings occur in nature; that is, one female may pair with more than one male.

Geneticists who are interested in the opportunities which this species provides, but unacquainted with its forms, should refer to Eltringham (1910), where they will find an excellent account of the more important of them, accompanied by admirable illustrations. Thus, in the majority of instances, it will only be necessary to give brief descriptions here. On the other hand,

it is essential to indicate the distribution and relationships of the different races, otherwise this account would be unintelligible.

The genetics of *P. dardanus* should in the future prove an exceedingly fruitful study, but clearly the first step is to make the work already accomplished available to students, and to analyse it so far as is possible. It will be valuable also to indicate how future research may be carried out to advantage, and what special precautions should be taken in conducting it. These are the objects of the present paper.

Dr. Karl Jordan has kindly informed me that in strict accordance with the International Code of Zoological Nomenclature, the name *Papilio dardanus* Brown, is not valid for this butterfly, and *P. cenea* Stoll, should be adopted for it. As, however, there is at least some hope that it may be possible to make an exception and save *P. dardanus* for the species, in the present paper I have, on his advice, retained this name, by which it is so well known. References to the original descriptions of most of the forms will be found in Seitz (1925). Only those which cannot be obtained from that work are given here.

My friends in the Hope Department of Entomology, Oxford, have given me help without which an account such as this could never have been written. Sir Edward Poulton, F.R.S., has placed in my hands numerous records of breeding experiments upon *P. dardanus*, and his unrivalled knowledge of its mimicry has made his advice invaluable. Under his direction, five-sixths of the known bred material of this species have been amassed in the Hope Collections. To these, now in the care of Professor Hale Carpenter, M.B.E., D.M., I have had constant access. Furthermore, Professor Carpenter's own helpful co-operation, and his personal knowledge both of this insect in nature and of the districts which some of its most interesting forms inhabit, have been of the greatest benefit to me. Dr. H. Eltringham, F.R.S., has been so good as to execute the beautiful painting represented on pl. 1.

I am greatly indebted to Professor R. A. Fisher, F.R.S., for his kindness in reading the typescript of this paper and in making a number of valuable suggestions. I wish to express my grateful thanks to Dr. Karl Jordan, F.R.S., for examining specimens of *P. dardanus* from S.E. Rhodesia, and giving me his opinion on their affinities (p. 441). I am indebted to the Keeper of Entomology at the British Museum (Natural History) for most kindly giving me facilities for examining the bred families of this butterfly in the National Collection. Dr. R. Hanitsch, Hon. M.A., has given me help for which I am most grateful.

A number of entomologists have devoted much time and labour to breeding *P. dardanus* in Africa, and it is a pleasure to express my great appreciation of their work. In particular, Dr. V. G. L. van Someren has conducted extensive experiments on the subspecies *polytrophus* which have provided an exceptional amount of data. Very valuable results have also been obtained by Mr. C. F. M. Swynnerton, Mr. W. A. Lamborn, O.B.E., Canon K. St. A. Rogers, Professor G. D. H. Carpenter, Miss M. E. Fountaine, and Mr. G. F. Leigh. In addition, Dr. C. A. Wiggins' vast unselected collection from the neighbourhood of Entebbe has been of great importance in establishing the proportion of mimics to models in that region. The extensive observations of Dr. van Someren, and a collection by Professor Carpenter, have provided similar information for the Nairobi and Kakindu districts respectively.

## 2. Races and distribution.

*P. dardanus* is found throughout the greater part of the Ethiopian Region, but not elsewhere. It forms a number of local races, and these generally merge

one into the other and interbreed at their boundaries. It is a large butterfly, varying in expanse from about 9 to 12·5 cm. The wings of the male are pale yellow, edged with black markings, and the hind pair are produced into the long " swallow-tails " typical of the genus *Papilio*. These are nearly always absent in the mimetic females, for the distasteful species which they copy are tailless. Not only do they thus imitate their models in shape and, often with marvellous effect, in colour and marking, but also in their habits of flight (Weale, 1874; Carpenter, 1913*a*).

In two regions, Madagascar and the Abyssinia–Somaliland district, the females possess tails. When non-mimetic, they closely resemble their respective males, except that they are all marked in varying degree with a black stripe along the costal margin of the fore-wings. This may extend from the base and curve backwards distally to end near the extremity of the cell (subsp. *meriones*), or it may be much reduced (subsp. *antinorii*). Trimen (1869) originally suggested that this bar forms the foundation of the complex pattern of the mimetic forms.

The various races will now be summarised in the order most convenient for study in this paper.

1. *P. dardanus meriones* Felder.

This is a primitive form inhabiting Madagascar. It is rather heavily marked with black, and there is a conspicuous black engrailed edging just within the hind-wings. Tails are present in both sexes and are black, tipped with yellow. The females are non-mimetic.

Another form, *humbloti* Oberthür, with male-like females, occurs in Grand Comoro. But it differs so much from any of the other races of *dardanus*, both in shape and in the distribution of the black markings, that it may well be a distinct species.

2. The *antinorii* group.

This occupies the extreme north-east of the insect's range. For a detailed account of it, students are referred to Carpenter (1935). The black markings are smaller than in any of the other races, and a characteristic yellow bay projects into the inner edge of the black band of the fore-wings in area 7. The females all possess tails and are mostly male-like, though a few are mimetic. These are the only instances of tailed mimics known in *P. dardanus*, other than a few exceptional specimens in which rudimentary tails are present. Two forms only may be recognised; a third inhabiting south-west Abyssinia was formerly separated as *hodsoni*, but must now be included with *antinorii*.

(a) *P. dardanus byatti* Poulton (1926). This is the most eastern, and is found in Somaliland. It has the least black of all, and may further be distinguished by the russet-brown underside. The few known females are non-mimetic.

(b) *P. dardanus antinorii* Oberthür, inhabits Abyssinia and Eritrea. The underside is either pale yellow, and relatively immaculate, or of a striking orange tone. The females are generally male-like. However, Stecker captured two mimetic females (with two male-like ones and seven males) on the shores of Lake Tana; these were described by Kheil (1890). One, *niavioides*, closely resembles a tailed *hippocoon* (p. 438), and the other, *ruspinae*, a tailed *trophonissa* (p. 438). Several other specimens of *niavioides* have been captured in recent years in south-western Abyssinia by Sir Arnold Hodson, K.C.M.G. (Poulton, 1928*b*). At Gore, western Abyssinia, he also obtained a single specimen of a tailed

form, *wienholti* Poulton (1928*a*). This is figured for the first time on pl. 1. It resembles *niobe* (see below) except that the brown areas are yellower in tone, and the patch at the base of the hind-wings is reduced in size so that it does not extend beyond the cell. It may be mimetic of *Bematistes epaea homochroa* Rothsch., and of *Acraea jodutta aethiops* R. and J.

These two forms of *antinorii* seem to grade into one another and, to the south-west of its range, *antinorii* itself probably interbreeds with the race next to be described. No breeding experiments have so far been carried out either on them or on *meriones*.

The remaining forms have been divided into five races by Jordan (1905). These he separates by the black markings of the males, and he has further shown that the male genital armature differs in the western and the eastern forms. He concludes, however, that the distinctions between them are not such as to prevent interbreeding; a view which is confirmed by the presence of intermediates at the geographical overlap and, to a limited extent so far, by breeding experiments (p. 446). It may be added that the female forms, and the proportions in which they occur, differ considerably in the various races, depending largely upon the models available in each region.

3. *P. dardanus dardanus* Brown.

This is the largest of the races of *dardanus*, and the males are less marked with black than those of any other group except *antinorii*.* It is found down the west coast of Africa from Sierra Leone to Angola, and far inland. It also spreads eastwards towards Uganda and Tanganyika Territory west of the Victoria Nyanza, where it merges into the next subspecies. As already mentioned, it probably breeds with *antinorii* further to the north-east.

*Female forms* :—(α) *hippocoon* Fab. This is black with white markings, and a series of irregularly developed white sub-marginal spots. There is a large white patch along the inner margin of the fore-wings, reaching as far as the first median nervure and generally spreading beyond it into area 2. A broad white sub-apical bar extends across areas 4–6, and there are small spots in areas 8 and 9, and one near the distal end of the cell. There is also a white patch at the base of the hind-wings, reaching only to the end of the cell or just beyond it.

Nowhere else is a single form so predominant in the species as is *hippocoon* from Sierra Leone to Calabar, for probably 99 per cent. of the females belong to it. From Cameroon to Angola the proportion must be a little less, owing to the occurrence of *niobe* and, eastwards, of *planemoides* (*q.v.*); but it still remains in great excess. It mimics *Amauris niavius niavius* L.

(β) *trophonissa* Auriv. A form similar in pattern to the last, save that the pale area always extends into the cell in the fore-wings and spreads considerably beyond it in the hind-wings. The white is, however, replaced by orange-brown except in the sub-apical bar and the spot near the extremity of the cell, and in all the sub-marginal spots. It is an excellent mimic of *Danaus chrysippus* L., but very uncommon.

(γ) *niobe* Auriv. is a modification of *trophonissa*, in which the orange colour completely replaces the white on the fore- as well as on the hind-wings, and is

* It may be mentioned that in the island of Fernando Po the pattern of the male is rather abnormal, and bears some resemblance to that of the male of subspecies *meriones* from Madagascar (Eltringham, 1917).

generally somewhat browner in tone. Furthermore, it never enters the cell in the fore-wings, so far as I have been able to ascertain. This slight, but apparently constant, difference in pattern does not seem to have been recognised, though it accords with the fact that the area occupied by orange-brown pigment is smaller in the model of *niobe* than in that of *trophonissa*.

This form mimics *Bematistes tellus* Auriv.* and, in the present subspecies, is found sparingly within the range of its model: from Cameroon to Angola and across the Congo basin. Further to the north-west it is only known as a rare aberration.

(δ) *dionysos* Doubl. is a very uncommon form confined to this race. It is approximately of the *hippocoon* pattern, with the white area of the hind-wings enlarged and replaced by lemon-yellow. The black markings on the fore-wings are very variable, and may even be so reduced as somewhat to resemble those of the male-like female of subsp. *meriones*. It has been suggested that *dionysos* is somewhat mimetic of *Amauris fenestrata* Auriv. But the resemblance is poor, the supposed model exceedingly rare, and the distribution of the two not at all co-extensive. Furthermore, the variability of *dionysos* suggests that its pattern is not favoured by selection (p. 452). Thus we must regard this form as non-mimetic, an opinion with which Poulton (1916 : 43) is in agreement.

(ε) *planemoides* Trim. is found occasionally from Angola eastwards. It will be discussed under the next subspecies, in which it is much commoner.

4. *P. dardanus* (Transitional).

The males resemble those of the previous race, but the genital armature is intermediate between that of *dardanus dardanus* and of the eastern forms. It is found in Uganda and Tanganyika Territory west of Lake Victoria and merges into *dardanus dardanus* further westwards.

*Female forms*:—(α) *hippocoon*.

(β) *trophonissa*.

(γ) *niobe*. This is actually more frequent than *trophonissa* in this subspecies, for its model is here abundant.

(δ) *carpenteri* Poulton (1929*b*). This is a rare form of *niobe* in which the brown markings spread over the greater part of the wings. The black pigment is reduced in the same manner, and almost to the same degree, as in *dorippoides* (*q.v.*, p. 443; *see also* p. 455).

(ε) *planemoides* (pl. 4, fig. 2) is quite common in the transitional race, but is found elsewhere only as a rare straggler, often with incompletely developed markings. The wings are black, with a broad curved orange bar across the whole width of the primaries from the costa to the inner margin, and a white area at the base of the secondaries, extending just beyond the cell. It mimics *Bematistes poggei* Dew., the male of *B. macarista* Sharpe, and perhaps the female form *aurivillii* Staud., of *Acraea alciope* Hew.

(ζ) *swynnertoni* Poulton (1929*b*) is an uncommon and incompletely developed form of *planemoides* in which the base of the hind-wings is pale yellow, while the orange bar on the fore-wings is more or less interrupted by black scales (*see also* p. 443).

(η) *cenea* Stoll. This form, so characteristic of the eastern races of *dardanus*, reaches its western limit here. It is black, with a yellow patch at the base of the hind-wings, extending just beyond the cell, and five rather small

* A female form of *Acraea jodutta* Fab., may also act as a model for it in some districts.

spots on the fore-wings, varying from yellow to white. The largest of these is situated in area 2, and it develops the deepest shade of yellow. The others are in areas 4, 6, and 8, and in the cell. There is also a series of rather irregular whitish sub-marginal spots on both fore- and hind-wings. It mimics *Amauris echeria* Stoll, in which the fore-wing spots vary in colour in a similar manner, and *A. albimaculata* Butl., in which they are always white.

($\theta$) *leighi* (p. 441) has been found once or twice in this subspecies.

The proportions in which these female forms occur in the transitional race can be estimated with some confidence. For several years Dr. C. A. Wiggins, C.M.G., made a large and completely unselected collection of Lepidoptera in the neighbourhood of Entebbe at the north-west corner of Lake Victoria, with the object of ascertaining the numerical ratios of models to mimics in that district. It contained 116 females of *P. dardanus* distributed with the following frequencies:—

| | | | |
|---|---|---|---|
| *hippocoon* | 70 | (60%) | |
| *planemoides* | 21 | (18%) | (21·5%) |
| *swynnertoni* | 4 | (3·5%) | |
| *cenea* | 8 | (7%) | |
| *niobe* | 8 | (7%) | |
| *trophonissa* | 5 | (4·5%) | |

Professor Carpenter also made a smaller but similarly unselected collection further to the south, at Kakindu, in Buddu, close to the southern frontier of Uganda, and thirty miles west of the lake. It contained 27 females of *P. dardanus*: there being 9 *hippocoon*, 9 *planemoides*, 4 *cenea*, 2 *niobe*, 1 *trophonissa*, and 2 intermediate between *planemoides* and *trophonissa*. It is hardly to be expected that the proportions should correspond in these two collections, for one is small, and they were made in different localities. It will, however, be noticed that *hippocoon* and *planemoides* are the commonest forms in each. These valuable results have not previously been published.

The two races last described constitute the western *dardanus* group. The three which follow belong to the eastern division of the species.

5. *P. dardanus tibullus* Kirby.

This is found for an uncertain distance north of the Mombasa district, and extends southwards to Delagoa Bay. The males are more heavily marked than in any of the other races.

*Female forms*:—($\alpha$) *cenea*.

($\beta$) *hippocoonides* Haase. This resembles *hippocoon*, except that the white area in the hind-wings is larger. It thus follows the eastern form of its model *Amauris niavius dominicanus* Trim., in which this area is similarly extended.

($\gamma$) *natalica* le Cerf (1924). A form of *hippocoonides* in which the pale areas are ochreous in tint. It is not mimetic, and may be regarded as a rare aberration.

($\delta$) *trophonius* Doubl. This corresponds to the western *trophonissa*, and only differs from it in the faintness of the dark internervular rays on the hind-wings. In the fore-wings the orange-brown pigment is often slightly more restricted, so that it does not enter the cell; but this is not a constant feature.

($\epsilon$) *salaami* Suf. is a modification of *trophonius* in which all the paler mark-

ings are orange. It therefore represents the western *niobe*, but is very much rarer; and in this region there is no known model that could protect it.

(ζ) *leighi* Poulton (1912) is a rare non-mimetic form showing some approach to *planemoides*. The pattern of the fore-wings is somewhat variable, but is approximately that of *cenea*, with the sub-apical bar of *hippocoonides*. The colour both of this bar and of the spots is a rich fulvous. The hind-wings have the pattern of *cenea*. The sub-marginal spots are fulvous, and the basal area may either be of the same colour or pale yellow. A somewhat aberrant specimen is represented on pl. 4, fig. 4.

The proportions of the more important female forms of subspecies *tibullus* may be estimated roughly from a large collection of butterflies " made nearly indiscriminately " by Mr. C. F. M. Swynnerton at Chirinda (S.E. Rhodesia). It contained 22 *hippocoonides*, 1 *cenea*, and 1 *trophonius* (Poulton, 1908). The experience of Lamborn (1918) in another part of its range helps to confirm this estimate. Collecting for some weeks at Tanga, on the coast at the extreme north of Tanganyika Territory, he at first found no form but *hippocoonides*, and remarked on the abundance of its model. Later, however, he saw a specimen both of *cenea* and of *trophonius*.

The southern specimens from Chirinda, to which reference has been made, are somewhat intermediate between the present race and that next to be described. This is shown by the less heavy development of the black markings on the hind-wings of some of the males. Dr. Karl Jordan, to whom I submitted them for examination, considers that they are a form of *tibullus* transitional towards the subspecies *cenea*, rather than the reverse. Furthermore, the proportions in which the female forms occur accord with those of the former race, in which *hippocoonides* is everywhere in excess, and differ strikingly from the latter.

6. *P. dardanus cenea* Stoll.

This race inhabits South Africa, northwards to Delagoa Bay. It is rather smaller than *tibullus*, with somewhat more rounded wings. The males are less heavily marked with black, but much more so than those of *dardanus dardanus*. Their pattern is subject to considerable variation.

It is unfortunate that the name *cenea* is at present applied to a race as well as to one of the numerous female forms occurring both in that and in other races. Its application must therefore be carefully distinguished.

*Female forms* :—These are the same as in *tibullus*. Their proportions, however, are quite different, for the *cenea* form of female is now predominant. They have been estimated by Leigh (Poulton, 1929*a*), who obtained 152 females by breeding from larvae found wild in the Durban district. These were distributed as follows :—

| | | |
|---|---|---|
| *cenea* . . . . . | 129 | (85%) |
| *hippocoonides* . . . . | 14 | (9%) |
| *trophonius* . . . . . | 6 | (4%) |
| *leighi* . . . . . | 3 | (2%) |

Poulton points out that the proportion of *leighi* thus obtained is certainly too high. Leigh had probably found several larvae from the same brood, laid by a chance female of this variety. However, it is less rare than in subsp. *tibullus*. It may be added that the forms *natalica* and *salaami* both occur in this race, but very infrequently.

7. *P. dardanus polytrophus* R. and J.

In distribution, this subspecies occupies a position between the transitional race and *tibullus*. It inhabits the high mountain region in the centre of Tanganyika Territory and in Kenya Colony on the south and east sides of the Victoria Nyanza. The majority of the known specimens come from Nairobi, but the most aberrant are found on the Kikuyu Escarpment (6,500-9,000 feet). It is the smallest of the races of *dardanus*. The males resemble those of the west in marking, but their genital-armature is that of *tibullus*.

This subspecies is most conveniently described last, instead of between those to which it is allied, for the mimicry of the female forms is often imperfectly developed. Owing partly to the rarity in these mountain districts of the species which serve it as models elsewhere, the various female forms, so constant in other areas, are here exceedingly variable (Section 4). Indeed they often show an approach to the ancestral male-like forms. This may be recognised in three ways. First, the amount of black pigment on the wings is often reduced. Secondly, females with rudimentary tails are sometimes found. Thirdly, they may possess a certain amount of the yellow pigment of the male, present also in the male-like females of subspecies *meriones* and the *antinorii*-group, but never in the females of the other races so far described. This point requires a short explanation. Yellow pigment is often developed in the mimetic females, and may sometimes bear a close superficial resemblance to that of the males. The latter, however, is fundamentally distinct. This is shown by the fact that it fluoresces in ultra-violet light (Cockayne, 1924), while no other pigments produced by *dardanus* do so. Thus it is possible to determine whether a yellow patch on a *polytrophus* female contains the male pigment, even if only in a few scattered scales.

*Female forms* :—Although the pattern of the males is more of the western type, that of the females is mainly eastern. Following the excellent suggestion of Poulton (1924*b*), the incompletely developed forms corresponding to the different mimics will be grouped together with the prefix *proto-* added to each. These may include several named varieties, but I shall ignore minor distinctions except where sharply defined : the present purpose being to make a classification which can usefully be employed for genetic purposes.

($\alpha$) *cenea.*

($\beta$) "*proto-cenea.*" This includes all specimens of *cenea* which possess fluorescent yellow pigment (pl. 4, fig. 10).

($\gamma$) *hippocoonides.* Although the females of this form are predominantly eastern in character, intermediates between it and the western *hippocoon* are sometimes found.

($\delta$) "*proto-hippocoonides.*" A form comprising all specimens in which either the pattern is intermediate between true *hippocoonides* and the male-like females, or fluorescent yellow pigment is present : generally the two conditions are combined. It includes *trimeni* Poulton, and the more extreme *dionysoides* Auriv.

($\epsilon$) *trophonius.* This is much rarer than the following modification of it.

($\zeta$) "*proto-trophonius.*" In the fore-wings the black markings are imperfect and variable, as in "*proto-hippocoonides,*" while the orange-colour of *trophonius* does not extend to the anterior edge of the large pale area above the inner margin. Fluorescent yellow pigment is developed in all the areas which are white in normal *trophonius*. The form is known as *lamborni* Poulton (1917) (pl. 2).

($\eta$) "*proto-salaami.*" In the true *salaami* the distribution of the black

markings is the same as in *trophonius*, while all the lighter areas are reddish-brown. I am doubtful if this precise form occurs in *polytrophus*. However, various modifications of it are quite common. In all of them the small spot in area 8 of the fore-wings, which forms the anterior end of the sub-apical bar, is yellowish or even white, and stands out distinctly from the other markings, as does a similar small yellowish area at the proximal end of the cell-spot. Occasionally the resemblance to *salaami* itself is perfect in other respects, the black markings having the same distribution as in *trophonius* (pl. 3, fig. 4, is of this form, except that the sub-apical bar is confluent with the spot in the cell). More often, however, they depart from this pattern. Such variation can take place in either direction. The amount of black may be increased, as in *poultoni* form. n. (*see* Appendix and pl. 3, figs. 1 and 2), or progressively diminished down to *dorippoides* Trim. (1908) (pl. 3, figs. 6–8). In the latter form it is wholly replaced by the reddish tint, except along the borders. On the fore-wings black pigment also remains in a small area at the tip, and in some markings along the costa and within the cell, while there is generally some slight clouding in the discal area. Even in this condition, the position normally occupied by the spot in area 8 can generally be distinguished as a patch in which the ground-colour loses its reddish tone and becomes paler. These "*proto-salaami*" forms appear to be non-mimetic (*see* pp. 454–5).

(*θ*) *planemoides* (pl. 4, fig. 2).

(*ι*) "*proto-planemoides.*" This includes any imperfectly developed form of the above, in which the bar on the fore-wings is sub-divided by intrusions of the dark ground-colour (pl. 4, fig. 3). When the resulting fore-wing spots are yellowish, instead of deep fulvous, and the basal patch of the hind-wings is yellowish or white, it is known as *mixtus* Auriv. (1907). This is to be distinguished from *swynnertoni* (p. 439), in which the fore-wing spots are of the normal deep fulvous and the base of the hind-wings always pale yellow.

It is fortunately possible to estimate the frequency of the *polytrophus* forms at Nairobi, as Dr. V. G. L. van Someren kept a careful list of all the female specimens of *P. dardanus* seen or caught in this neighbourhood for several months in 1923. His records form part of the valuable unpublished data which Sir Edward Poulton has placed at my disposal. They may be summarised as follows :—

| | | |
|---|---|---|
| *cenea* | 47 | 65 |
| "*proto-cenea*" | 18 | |
| *hippocoonides* | 44 | 53 |
| "*proto-hippocoonides*" | 9 | |
| *trophonius* | 1 | 17 |
| "*proto-trophonius*" | 16 | |
| "*proto-salaami*" | 15 | 15 |
| | 150 | |

Thus the imperfectly developed forms, so rare elsewhere, here reach 38 per cent. of the total.

It is curious that neither *planemoides* nor its modifications are included in this sample, for they do not seem rare in collections from the district.

*Note.*—Some of the abnormal forms, which comprise a considerable part of the population of *polytrophus*, occur as rare aberrations in the neighbouring subspecies. Thus *trimeni* was first described by Poulton from a specimen caught in the Zanzibar district, *poultoni* has been taken more than once near

Mombasa, and "*proto-planemoides*" on the coast near Malindi; these all being within the range of subspecies *tibullus*. Also, as already mentioned, *swynnertoni* is known in the transitional race.

Many minor varieties of *P. dardanus* have received names which have been omitted from the foregoing account as irrelevant to the purpose of this paper. The majority of them may be obtained by reference to Aurivillius (1907), le Cerf (1924), and Seitz (1925).

### 3. Genetics.*

Sir Edward Poulton (1915, 1920) has tentatively discussed the possible genetic relation between some of the female forms of *P. dardanus*. He put forward the very reasonable suggestion that *hippocoonides* is recessive to *cenea*, and to some of the rarer forms. Apart from this, no attempt has been made to analyse it.† At present the task presents three main difficulties. First, the one inherent in the species, that the males are monomorphic, so that their constitution cannot be determined by observation. For the factors determining the female forms are sex-controlled and autosomal, being inherited equally through either sex but inactive in the male gene-complex. Secondly, nearly every family so far obtained is the product of a female fertilised in nature. There is thus the possibility that it may have paired more than once: this almost certainly occurs not uncommonly, and leads to the production of broods of mixed origin (pp. 450–1). Thirdly, the majority of the existing bred families belong to the *polytrophus* race. The female forms of this subspecies being numerous and complex, it provides by far the least suitable material for preliminary study. The following account must therefore be regarded as provisional, and alternative suggestions are put forward as a basis for future work.

There is some evidence for thinking that *dionysos* is a heterozygous form. On the only occasion that it has been bred (no. 7), a female *hippocoon* produced 8 *dionysos* and 9 *hippocoon* offspring. Although these numbers are small, they apparently represent segregation in equality. In order to test this suggestion, it must be determined to what extent they depart from the nearest 3 : 1 ratio; that is 3 *hippocoon* to 1 *dionysos*, being the one possible on the alternative assumption that *dionysos* is recessive. This deviation is measured by $\chi^2 = 4{\cdot}41$ for one degree of freedom. In other words, it is 2·1 times its standard error, a magnitude which would usually be taken as significant. Thus we are fairly safe in regarding this as a back-cross.

Now 0·5 per cent. of the western females probably represents an upper limit for the frequency of *dionysos*. Consequently, if it were a recessive, only 13 per cent. of the population would be heterozygotes, and *hippocoon* crosses yielding it in a 3 : 1 ratio would be twenty-six times as common as those in which it appears in a 1 : 1 ratio. In these circumstances, therefore, one would not expect that the only instance on record should be of the latter type, as it seems to be. On the other hand, if *dionysos* is a heterozygote, as here suggested, all

* The numbered families refer to those tabulated on pp. 458–62. Entomologists not familiar with genetic terms may refer to Ford (1934), where they will find them explained.

† Goldschmidt (1927 : 187–91) gives a theoretical interpretation of the genetics of *hippocoonides*, *trophonissa*, and *cenea* in terms of two pairs of allelomorphs; one controlling the rate of melanin production, and the other the colour of the lighter areas. However his conclusions are reached without reference to breeding experiments, and his suggested tract for the spread of melanin does not conform to that actually followed by this pigment; for this can be ascertained by an examination of intermediate specimens,

families should segregate in equal numbers when both it and *hippocoon* arise as the offspring of a *hippocoon* parent.

It would, however, be arguing in advance of the facts if one were to describe *dionysos* as a dominant. It is important to restrict this term to the condition when the heterozygote resembles one of the homozygotes. In the present instance it seems that *hippocoon* may be regarded as recessive. Giving *dionysos* the above frequency of 0·5 per cent. of the females or less, then homozygotes of this form must be in the proportion of 1 : 155,000 at most. At so low a frequency there is no justification for supposing that the heterozygotes and homozygotes have been modified to resemble one another, and the latter may even be inviable (pp. 457–8).

It is idle to speculate on the precise relation of *niobe* to *trophonissa*, though no doubt this could be determined by experiment. It may, however, reasonably be assumed that the two are not independently controlled, but that the one is converted into the other by a single "modifying factor." For these are certainly polymorphic forms, deriving benefit from a resemblance to different models. It is therefore probable that a simple genetic mechanism exists which can act as a switch in maintaining them in optimum numbers in the population. A similar conclusion in regard to the control of *swynnertoni* and *planemoides* is less probable; for the former may merely be an incompletely developed form of the latter. It may thus arise from an imperfect adjustment of the gene-complex. On the other hand, it seems possible that *swynnertoni* profits from a resemblance to one of the female varieties of *Acraea alciope aurivillii* (p. 453). If so, the points in which it differs from *planemoides* may well have been selected to fall within the control of a single factor.

There is, unfortunately, not enough evidence to determine the relation of *planemoides* even to *hippocoon*, the commonest of the forms with which it flies. So far it has only been possible to breed from it three times. Having regard to the proportions in the transitional race, families no. 8 (2 *cenea*, 2 *planemoides*, 2 *hippocoon*) and no. 9 (3 *planemoides*, 7 *hippocoon*) could have been obtained whether it were recessive or dominant * to *hippocoon*. No. 99 is a *polytrophus* female; and the forms of this subspecies are far too complex to draw any conclusions from a single family, perhaps having multiple paternity.

The genes controlling the less common forms of *P. dardanus* will not often be brought together in nature. It is quite possible therefore that some of them may combine to produce a confused result, for their product will rarely be exposed to selection. There is some support for this view, for Poulton (1929*b*) considers that *carpenteri* combines the patterns of *planemoides* and *trophonissa*. Carpenter (1916) was able to breed from a specimen of this form and obtained two female offspring only, one a normal *planemoides* and the other a normal *trophonissa* (no. 10). Thus it seems possible that the respective genes acting together had given a mixed effect. On the other hand, since approximately 18 per cent. of the transitional race are *planemoides* and 4·5 per cent. are *trophonissa* (p. 440), just under 1 per cent. should, on this hypothesis, be *carpenteri*. This result certainly seems unexpectedly high, for, in fact, it is a great rarity. Furthermore, it is reasonable to suppose that *niobe* could be substituted in this combination, as it differs little from *trophonissa* except in the absence of white on the fore-wings, which is not present in *carpenteri*. Since *niobe* occurs as approximately 7 per cent. of this population, the proportion of *carpenteri* should thus be raised to about 2 per cent. It must also be borne in mind that this form

* This term may safely be used with these higher frequencies, subject to the qualification discussed on pp. 457–8.

is phenotypically identical with certain of the modifications of "*proto-salaami*" in subspecies *polytrophus* (p. 455), and it may quite possibly be genotypically identical with them also. These are certainly not due to a combination of *planemoides* and *trophonius* (pp. 449–50), whose appearance in no. 10 may be the result of ordinary segregation, irrelevant to the pattern of the female parent.

Turning now to the eastern races, *natalica* is likely to be due to a heterozygous modifier of *hippocoonides*. I do not know the frequency of this form, but it is certainly very rare; it seems to be caught about as often as is *dionysos* on the west coast, or even more infrequently. Consequently, if recessive, only 13 per cent. of the population or less would be heterozygotes. The chances would thus be against obtaining *natalica* offspring from a female of that form mated at random, as in fact occurred on the only occasion that it has been bred (no. 14). The number of offspring (5 *natalica*, 3 *hippocoonides*) is unfortunately too small to determine whether they are segregating in a 3 : 1 or a 1 : 1 ratio.

There is good reason for thinking that *hippocoonides* is recessive to the *cenea* form of female. In *tibullus*, one may estimate that the frequency of the latter is not greater than 4 per cent. (p. 441). Yet the two *cenea* females of this subspecies from which families have been obtained (nos. 11 and 12) have each produced their own form as well as *hippocoonides* (*see* p. 451). Now if *cenea* were recessive, not more than 36 per cent. of the males should be carrying genes for it, and the result actually obtained would be less likely. Furthermore, the 22 *hippocoonides* females of subspecies *tibullus* which have produced families (nos. 15–36), have given nothing but their own form. Although the numbers in some of these are small, this result is rather unexpected if *hippocoonides* were a dominant. For in that event, 36 per cent. of both sexes should be heterozygotes, while an additional 4 per cent. of the males should be homozygous for the *cenea* genes.

More important, however, is the evidence to be derived from the only experiments on inter-racial crossing in *P. dardanus* known to me. Mr. C. F. M. Swynnerton (1919) obtained pupae of subspecies *cenea* from Natal, where *cenea* is the commonest form of the female (p. 441), and crossed some of the resulting females with males of *tibullus* subspecies at Chirinda, where it is rare. As already mentioned, one may perhaps be justified in giving it a frequency of about 4 per cent. in this district, and this accords with the view of Poulton (1915).

On emergence, all the Natal females proved to be of the *cenea* form. Swynnerton crossed one of them with a Natal male, the offspring being again all *cenea* (no. 119). Another he mated with a male of the *tibullus* race, and obtained a single *cenea* female in F1 (no. 120). A third, also crossed with a Chirinda male (race *tibullus*), gave 10 females, all *cenea* (no. 121). By mating the imagines from a further pair of Natal pupae, an F1 including both *cenea* and *hippocoonides* was produced (no. 122). Two of these he crossed with males of the *tibullus* race. One, a *cenea* (no. 123), gave both *cenea* and *hippocoonides* offspring (2 : 3), while the other, a *hippocoonides* (no. 124), produced 6 females, all of its own form.

On either hypothesis, the majority of the males of subspecies *tibullus* are homozygous *hippocoonides*. The results show that, mated with them, *hippocoonides* females produced their own form only, while *cenea* females could produce either their own form alone, or both. Thus one again reaches the conclusion that *hippocoonides* is recessive to the *cenea* form. It is important to notice that these experiments of Swynnerton's are of exceptional value, since it is known that each female had mated with a single male only (p. 456).

In view of the probable frequency of mixed matings, the results obtained by breeding from wild females of the subspecies *cenea* are necessarily more confused. For a presumed dominant is here the commonest form, while some of those in a minority are less rare. However, no. 49 (in which a *hippocoonides* female produced 13 offspring, all of the *cenea* form) rather strongly supports the hypothesis so far advanced. The four families here tabulated are the only ones in this subspecies in which the *cenea* and *hippocoonides* forms have segregated alone.

| No. of family. | ♀ Parent. | Offspring. | |
|---|---|---|---|
| | | *cenea.* | *hippocoonides.* |
| 37 | *cenea* | 16 | 1 |
| 38 | ,, | 24 | 3 |
| 40 | ,, | 21 | 2 |
| 52 | *hippocoonides* | 13 | 2 |

The first three of them also accord with a simple interpretation in which *cenea* is dominant. The proportion of *hippocoonides* is, however, even smaller than it should be on a single-factor basis. Accepted at their face value, therefore, these data suggest a slight genetic complication. But the deviation is more probably due to multiple matings, as it seems to be in the last family (no. 52) where the *cenea* form is still in excess, though a 1 : 1 ratio is to be anticipated.

There is no indication that the yellow- and white-spotted forms of *cenea* are under different major genetic control. They are probably due to the action of minor modifiers, or they may even be phenotypic. I have, however, separated them in the tables on pp. 458–62, in case the information should ever become useful in the light of future work.

At present sufficient evidence is not available to decide if *trophonius* is dominant or recessive to *hippocoonides*, for the facts appear conflicting. The absence of any *trophonius* offspring in the *hippocoonides* families 15–36 seems to favour its dominance. For about 4 per cent. of the Chirinda females are of this form (p. 441), so that, if recessive, 32 per cent. of the population would be heterozygous, and a further 4 per cent. of the males homozygous, for *trophonius* factors. In such circumstances one might perhaps have expected *trophonius* to appear among the offspring of these twenty-one *hippocoonides* females, as 14 per cent. of them should produce it. More families like no. 13 (P1♀, *cenea*; F1, 4 *trophonius*, 3 *hippocoonides*) would also support the dominance of *trophonius* but, having regard to the percentages, this single instance is quite inconclusive.* On the other hand, no. 45 provides rather good evidence in favour of the contrary view. Here a *trophonius* female produced no offspring of her own form, 11 *hippocoonides*, and 7 *cenea*. The latter may be neglected for the present purpose, since the families in which all three occur (nos. 43, 44, 46, 48, 50, 51) do not suggest any close linkage. Some of the 11 *hippocoonides*, therefore, should certainly have been *trophonius* if the latter were dominant; for then, given that any *hippocoonides* appear at all, a 1 : 1 ratio would be expected between them. It is particularly to be noticed that the possibility of mixed matings does not affect this argument. It is im-

* *P. d. hippocoonides* is recessive to "*proto-salaami*" (pp. 449–50). Judging by pattern alone, the latter may be a modification of *trophonius*, but there is no evidence for this.

material whether the *hippocoonides* are the offspring of one or more male parents; the *trophonius* gene of the mother must in any event be received by half of them. Thus the relation of *trophonius* to *hippocoonides* cannot yet be decided for certain, though it appears more probably to be recessive than dominant to it.

It does not seem that any opinion can yet be formed on the genetics of *leighi*. The matter would be particularly interesting, and families 39, 43, and 44 may perhaps become of value in the future when further work can be done on this subject.

An important problem is raised by the inter-relation of *cenea*, *hippocoonides*, and *trophonius*. These are the most widespread of the mimetic forms. They exist together in three of the races (*see* pp. 439–41), and must be balanced in optimum numbers in them. One may feel confident therefore that they are controlled by a simple genetic mechanism. In colour and pattern, *trophonius* is only a modified *hippocoonides*, while *cenea* is quite distinct. Thus it is not unreasonable to suggest that the *trophonius* gene may modify *hippocoonides* but be inoperative in *cenea*, this being the same simple type of factor-interaction which maintains the three female forms of *Papilio polytes*, analysed by Fryer (1913). Accepting the previous conclusion that *hippocoonides* is recessive to *cenea*, the above view necessitates that *trophonius* should behave as a recessive to *cenea* also. As has been seen, its precise relation to *hippocoonides* must be left in doubt, but this is not very material to the present purpose.

On these assumptions, when either a *hippocoonides* or a *trophonius* produces all three types of offspring, the number of *cenea* should equal the sum of the other two classes. The existence of multiple matings, however, should on the average tend to increase the class which represents the commonest form in the district, this being *cenea* in the six instances at present available.

| No. of family. | ♀ Parent. | Offspring. | | |
|---|---|---|---|---|
| | | *cenea*. | *trophonius*. | *hippocoonides*. |
| 43 | *trophonius* | 22 | 4 | 2 |
| 44 | ,, | 9 | 4 | 2 |
| 46 | ,, | 12 | 1 | 5 |
| 48 | *hippocoonides* | 8 | 3 | 3 |
| 50 | ,, | 14 | 2 | 4 |
| 51 | ,, | 17 | 8 | 11 |

Of these, nos. 44, 48, and 51 are obviously in accord with the expectation, while the departure from it of no. 46 is not significant ($\chi^2 = 2{\cdot}00$). In no. 50 the divergence is doubtfully significant ($\chi^2 = 3{\cdot}20$), and in no. 43 it is certainly so. But, in both of these, the excess is in favour of *cenea* which, as may be seen, does not necessarily indicate a genetic complication.

Of the two families in which *cenea* and *trophonius* have segregated alone, no. 41 (P1♀, *trophonius*; F1, 6 *cenea*, 1 *trophonius*) is inconclusive, while no. 47 (P1♀, *trophonius*; F1, 2 *cenea*, 22 or 23 *trophonius*), unlike those previously discussed, appears to indicate the dominance of the latter. But, when taken in association with the other relevant families, it seems abnormal on any simple genetic hypothesis: I am strongly inclined to think that the female parent had mated twice.

The value of the work which has been done on subspecies *polytrophus* is at present largely potential. It may, however, become of importance when the

genetic relationships of the fully developed female forms have been established, and some estimate has been made of the frequency of mixed matings in nature. In any event it should be supported by further crosses between bred specimens, in which multiple paternity can be excluded.

With one partial exception, it does not seem possible at present to draw definite conclusions in regard to the genetics of these more complex *polytrophus* forms. On the other hand, an examination of families 54 to 118 will show that all are genotypic, and that they are probably inherited on fairly simple lines. For, ignoring those of which very few have been bred, as "*proto-hippocoonides*" and *swynnertoni*, each form appears significantly more often among the progeny of its own type of female than among those of the other varieties. Thus the *cenea* families (54 to 72) have produced 91 *cenea* and 36 "*proto-cenea*" (28 per cent. of the latter form); while the "*proto-cenea*" families (73 to 84) have given 31 *cenea* and 49 "*proto-cenea*" (61 per cent.). If it be supposed, as is reasonable, that the "*proto-cenea*" and the *cenea* forms are produced respectively by genotypic modifications of the same gene, the evidence of families 54 to 84 and 102 to 115 accords quite well with the view already reached that *hippocoonides* is recessive to *cenea*. No. 73 (P1♀, "*proto-cenea*"; F1, 1 "*proto-cenea*," 5 *hippocoonides*, 6 "*proto-hippocoonides*") is, however, exceptional for, even with such small numbers, the amount by which the two *hippocoonides* classes, taken together, exceed equality, appears significant ($\chi^2 = 8{\cdot}34$). It is impossible to say whether this departure from expectation is due to multiple matings or to some genetic complication introduced, perhaps, by the presence of "*proto-hippocoonides*." A further difficulty is raised by the offspring of a "*proto-trophonius*" female (no. 86), for these consist of 1 *cenea*, 7 "*proto-cenea*," 10 "*proto-trophonius*," 27 "*proto-salaami*," and 19 *hippocoonides*. It looks as if this had paired both with a male carrying "*proto-salaami*" (heterozygous for *hippocoonides*) and with one carrying *cenea* genes.

The four "*proto-trophonius*" females (85 to 88) have produced 132 female offspring, 34 being "*proto-trophonius*" (26 per cent.). All the other females of the *polytrophus* race have produced 601 female progeny, which include only 29 "*proto-trophonius*" (5 per cent.). Though segregation of a simple kind is here indicated, the genetics of this form presents a complication which it seems impossible to solve with the present data. A wild *cenea* female (no. 65) produced 20 *cenea* offspring, 13 being *cenea* and 7 "*proto-cenea*." Three of them were mated in captivity with their brothers. One, a *cenea* (no. 66) produced 7 *cenea* and 1 "*proto-cenea*" offspring. Another, a "*proto-cenea*" (no. 83), produced 4 female offspring only, all "*proto-cenea*"; while a third, also "*proto-cenea*" (no. 84), produced 5 "*proto-cenea*" and 8 "*proto-trophonius*." Now "*proto-trophonius*" certainly seems recessive to "*proto-cenea*," otherwise it should have appeared among the 20 offspring of no. 65 (if dominant, a minimum of half is expected); nor, for the same reason, can it be a recessive segregating as a back-cross. Thus, in F2, "*proto-trophonius*" must appear in one quarter of the offspring only. But 8 out of 13 are of this form in no. 84; a deviation which certainly seems significant ($\chi^2 = 9{\cdot}21$). It will be noticed that this family had been obtained by a mating in captivity, and it is therefore one of the few instances in which the paternity is not in doubt. It will be extremely interesting to learn the explanation of this anomaly when further controlled matings have been made.

"*proto-salaami*" (including its modifications *poultoni* and *dorippoides*) is rarer than *hippocoonides* (*see* p. 443), and is certainly dominant to it. Females of this form (nos. 89 to 98) have produced two types of families: all "*proto-*

*salaami*" (no. 92, with 18 offspring), or a 1 : 1 ratio of "*proto-salaami*" to *hippocoonides* (the totals are 33 : 27, no instance being inconsistent). No. 98 must be omitted, as the numbers (4 "*proto-salaami*," 3 "*proto-trophonius*") are too small to indicate to which class it belongs. If it is justifiable to assume that "*proto-trophonius*" is a modified *hippocoonides*, as the normal *trophonius* appears to be, no. 98 could be included (with the 2 "*proto-trophonius*" in no. 96), and the totals become 36 : 32.

The evidence which these families provide on the relation of "*proto-salaami*" to "*proto-trophonius*" and *cenea* (with "*proto-cenea*") is inconsiderable. However, the five others in which it occurs (nos. 62, 70, 80, 82, 86) may be taken into consideration with them. There is then some indication that it is dominant to "*proto-trophonius*," as is particularly suggested by no. 86 (P1♀, "*proto-trophonius*," F1, 8 *cenea*, 10 "*proto-trophonius*," 27 "*proto-salaami*," 19 *hippocoonides*). It is here assumed that the 8 *cenea* are due to a multiple mating, which is indicated by their abnormal proportion relative to *hippocoonides* (p. 449). Furthermore, nos. 70 (P1♀, *cenea*; F1, 24 "*proto-cenea*," 1 "*proto-salaami*," 4 *hippocoonides*) and 82 (P1♀, "*proto-cenea*"; F1, 13 "*proto-cenea*," 1 "*proto-salaami*," 4 *hippocoonides*) provide some evidence that this form is recessive to "*proto-cenea*" and therefore, probably, to *cenea*. These latter results are inconclusive, but the dominance of "*proto-salaami*" to *hippocoonides* seems established.

*P. d. poultoni* may rather safely be regarded as a genotypic modification of the normal "*proto-salaami*." Intermediates between the two are rare, but a family (no. 92) has been obtained from one of them. The 18 "*proto-salaami*" offspring formed a continuous series from one extreme to the other. But specimens which are not themselves intermediates have produced none. Thus the five *salaami* offspring of a *salaami*-like female (no. 96) were all similar to herself; while other females of the same kind, and of *poultoni*, have given only *poultoni* offspring among the "*proto-salaami*" forms (nos. 89 to 98).

Before ending this survey of the genetics of *P. dardanus*, a few questions of a more general nature remain to be considered.

It is not known how often females mate with more than one male, either in this or in any other butterfly. The occurrence seems to be generally admitted by entomologists, but data upon it are almost wholly lacking. Indeed it is very unlikely to be noticed, even if quite common, unless the matter were under special observation. A wax-like mass, secreted by the male (Eltringham, 1925), and moulded into a characteristic shape, is found after pairing on the abdomens of females in *Parnassius* and some other genera. Poulton suggested that it prevents more than one mating (Marshall, 1902), and Eltringham (1912) has endorsed this conclusion in *Acraea*. The evolution of such a mechanism in certain forms seems to suggest the frequency of this occurrence in normal circumstances. I have elsewhere drawn attention to an instance in which the Mendelian ratios demonstrate that a multiple pairing, suspected on other grounds, had in fact taken place in a female of the *wahlbergi* form of *Hypolimnas dubius* Beauv. (Carpenter and Ford, 1933 : 118). Since this was almost the only known instance in which it could have been detected, one may suppose that polyandry is very common in that species.*

* It is known that multiple matings occur also in moths. Onslow (1919) quotes evidence from crosses between *Tephrosia consonaria* and its black form *nigra* which establishes not only that they take place but that they give rise to broods of mixed paternity. He has himself shown that both sexes of *Abraxas grossulariata* can pair more than once.

In *P. dardanus* the matter may be approached statistically. The effect of multiple matings on segregating families must be, on the average, to increase the proportion of the commonest form in the district. That is to say, they should lead to an excess of *cenea* females in subspecies *cenea*, and of *hippocoonides* in subspecies *tibullus*. One must treat the families segregating in a 1 : 1 and a 3 : 1 ratio separately and, in view of the uncertainty of the genetic relations of some of the other forms, exclude all except those producing *cenea* and *hippocoonides* only. In subspecies *cenea* these are nos. 37, 38, 40, 45, and 52. No. 45 seems to be a back-cross, for the two types it contains appear in small numbers which do not differ significantly from equality (7 : 11), so that there is no reason to think it disturbed by multiple matings. No. 52 should be of the same nature, since the female parent is of the recessive form. One would therefore expect the offspring to appear in a 1 : 1 ratio; actually, however, the numbers are 13 : 2, with *cenea* in excess. The remainder apparently arise from crosses in which both parents are heterozygotes. The totals for the three are: 61 *cenea* and 6 *hippocoonides*—a clearly significant excess of *cenea* over the expected 3 : 1 ratio. Only two families of subspecies *tibullus* are available for study. No. 12 is quite useless, as we cannot even say if it is segregating in a 1 : 1 or a 3 : 1 ratio (2 *cenea*, 1 *hippocoonides*). The other, no. 11, is outstandingly different from anything obtained in the southern race, for here is a deficit of the dominant *cenea* form and an excess of the recessive *hippocoonides* (4 : 13).* The nearest probable ratio is one of equality yet, small as the numbers are, they strongly suggest a significant deviation from it ($\chi^2 = 4{\cdot}76$). There is thus rather good evidence in favour of multiple matings in the present species.

On the evidence of his valuable crosses between the subspecies *cenea* and *tibullus* (p. 446), Mr. C. F. M. Swynnerton reached the conclusion that *hippocoonides* is recessive to the *cenea* form, and he thought it possible to distinguish between the heterozygotes and the homozygous dominants. He says: "I am able, I think, to recognise complete *cenea* by the presence of dark shading at the base of the hind-wing under surface; incomplete *cenea* by the absence, complete or nearly, of this shading and by the presence, usually, of pale scales (whitish or yellow) below the main fore-wing spot—corresponding, that is, to the extension in *hippocoon* [*hippocoonides*] of the big hind-wing patch into the fore-wings. The underside difference is the constant one, or nearly so." On working through the large amount of material at my disposal, I have not been able to convince myself of the validity of this distinction. At first I made an attempt to separate heterozygous and homozygous *cenea* in my own data, but the classification was not always possible and led to inconsistencies. I therefore abandoned it, and have not endeavoured to score them separately in the tables on pp. 458–62.

There is no reason to doubt the genetic identity of the corresponding western and eastern forms. *trophonissa* and *trophonius* are hardly distinguishable except in size, for the difference between their pattern is minute, while *niobe* and *salaami* may respectively represent genetically similar modifications of them. *hippocoon* and *hippocoonides* are adapted to the geographical races of their model, but this involves an alteration only in the size of the white area on the hind-wings; in other respects they are identical. It may be supposed that selection, operating on the gene-complex, has adjusted the effects of the same factor to the needs of the different races.

* Future work may, however, show that the possibility discussed on p. 457 may have to be taken into account here. But, in the light of the crosses between subsp. *cenea* and *tibullus*, this is not at all likely.

### 4. The Variability of Subsp. *polytrophus*.

The genotypic variability of an organism is evidently in equilibrium between the effects of mutation and recombination, tending to increase it, and of selection, tending to diminish it. The selective advantage enjoyed by mimics will therefore stabilise their pattern. Consequently, a non-mimetic form like *dionysos* is much more variable than a good mimic like *hippocoon*, with which it flies. Poulton (1915, 1916) has insisted on this stabilising influence of selection, and I have elsewhere developed the concept from the genetic standpoint (Ford, 1934; Carpenter and Ford, 1933). Similarly the mimetic forms should themselves become variable if they occur in regions where their models are absent, or too rare to provide effective protection. There is good reason for thinking that this is, at least in part, responsible for the extraordinary breakdown in the mimetic adjustment of *P. dardanus* in its *polytrophus* race. For evidence is now available to show that the protected, and normally abundant, species which it copies are relatively rare in the mountainous districts in which this subspecies flies.

Dr. van Someren has recorded all female specimens of *P. dardanus*, and of their models, caught or seen in the neighbourhood of Nairobi for several months in 1923, and I am greatly indebted to Sir Edward Poulton for putting his data at my disposal. From these numbers can be obtained an estimate of the frequency of mimics relative to models in subspecies *polytrophus*. Fortunately the material exists for a comparison between this and the condition in one of the subspecies in which the mimetic forms are more fully developed, the transitional race, for Dr. C. A. Wiggins made a very large random collection in the Entebbe district. This material is preserved in the Hope Department of Entomology at Oxford, and I have counted the female specimens of *P. dardanus* and of their models which he obtained. The valuable results of these two workers are now published in full for the first time.* They allow a comparison of the relative proportions of the models to mimics in the two races, and of the stability of the mimic in each.

Transitional race (Entebbe).

| | Mimics. † D | Mimics. I | Mimics. T | Models. |
|---|---|---|---|---|
| *hippocoon* | 70 | 0 | 70 | 104 |
| *planemoides* | 21 | 0 | 25 | 781 |
| *swynnertoni* | — | 4 | | |
| *cenea* | 8 | 0 | 8 | 232 |
| *niobe* | 8 | 0 | 8 | 832 |
| | 107 | 4 | 111 | 1949 |

Imperfectly developed forms of mimic = 4% (3·6%).

Models for :—
*hippocoon* = *A. niavius* (104).
*planemoides* = *B. poggei* and ♂ *macarista* (571), *A. alciope* ♀ f. *aurivillii* (210).
*cenea* = *A. echeria* and *albimaculata* (232).
*niobe* = *B. tellus* (687), *A. jodutta* ♀ f. (123), *A. althoffi* ♀ f. (22).

* A portion of Dr. Wiggins' data has already been summarised by Poulton (1910).
† D = Developed form of mimic, I = Imperfect form of mimic, T = Total.

| *polytrophus* race (Nairobi). | | | | |
|---|---|---|---|---|
| | Mimics. | | | Models. |
| | D | I | T | |
| *cenea* . . . . . | 47 | 18 | 65 | 32 |
| *hippocoonides* . . . | 44 | 9 | 53 | 0 |
| *salaami* . . . . | 0 | 15 | 15 | 0 |
| | 91 | 42 | 133 | 32 |
| Imperfectly developed forms of mimic = 32%. | | | | |
| MODELS FOR :— *cenea* = *A. echeria* (28), *A. albimaculata* (3), *Pseudacraea leucretia* (1). | | | | |

These data show that, in the forms here considered, the imperfectly developed mimics are eight times commoner, and the models seventy times rarer relative to their mimics, in *polytrophus* than in the transitional race. But in the former subspecies, all the models are those for the *cenea* form. Even so, they are only half as common as their mimic (49 : 100). To make a just comparison, this proportion should be contrasted with the lowest ratio in the transitional race : that between *Amauris niavius* and *hippocoon*. Here the situation is reversed, the models being one-and-a-half times as common as their mimics (149 : 100). It seems established, therefore, that there is a deficiency of models relative to mimics in subspecies *polytrophus* as compared with a race in which the mimicry is more fully developed.

This result is comparable to that obtained by Carpenter (1932) in his study of the polymorphic mimic *Pseudacraea eurytus* L. and the various species of *Bematistes* which it copies. He obtained estimates of their relative abundance on the island of Kome, Lake Victoria, for three different years. When the proportion of models to mimics was high (over 70 per cent.), intermediates between the different forms of *P. eurytus* were uncommon, being 4 per cent. or less of those captured. When, however, the models were less common than the mimics, intermediates between the mimetic forms became quite frequent, varying from 11 to 30 per cent. of the *eurytus* population.

It is curious that an imperfect form of *planemoides*, that known as *swynnertoni*, should occur in the transitional race, in which its models are so abundant. This has been treated here as an imperfect mimic, in order that no unfair bias should be given to the data. But it is probable that, in reality, its pattern has a selective advantage from its resemblance to the form of *Acraea alciope aurivillii* in which the hind-wings are yellowish or tawny.

The mimetic relations of *trophonius* call for some comment. This form (or *trophonissa*) is found in all the races of *P. dardanus*. It is normally rather rare (5 per cent. or less), while its model is generally abundant. But the two do not really live in the same habitat. The *Papilio* is a forest butterfly while *Danaus chrysippus* is found in open country, so that they seldom fly together; hence, apparently, the rarity of the mimic. I have not included it in the present comparison, as the numbers of the model at Nairobi are not stated by Dr. van Someren : indeed the effective numbers (in the localities where *dardanus* is found) might be rather difficult to define. He merely remarks that " it is fairly plentiful at all times, but in more open parts and on the plains."

One would therefore have expected that the *trophonius* form would be as uncommon and as stable in subspecies *polytrophus* as it is in the other races. Actually its frequency is rather more than doubled (11 per cent.), and nearly every specimen is of the imperfect *lamborni* form. It is evident that in this mountain district the species is able to maintain itself without the help of accurate mimicry, while, in any event, the proportion of *trophonius* may well be too high relative to its model for stability. Furthermore, with so much genotypic variation occurring in the race, rather stricter selection than usual might be necessary to standardise a single form.

Professor Carpenter's smaller random collection (p. 440) in the Kakindu district (transitional race) also included models as well as mimics. His results were as follows :—

| Transitional race (Kakindu district). | | | |
|---|---|---|---|
| Mimics. | | Models. | |
| *hippocoon* . . | 9 | 5 | *A. niavius* |
| *planemoides* . | 9 | 6 | *B. poggei.* |
| *cenea* . . . | 4 | 27 | *A. albimaculata* (14), *damocles psyttalea* (12), *echeria* (1). |
| *niobe* . . . | 2 | 28 | *B. tellus* (24), *A. jodutta* (4). |
| | 24 | 66 | |

It will be seen that, though the models are much commoner than in subspecies *polytrophus*, they are considerably rarer than at Entebbe. However, unlike the other two collections, the numbers here are too small to place much reliance on relative proportion.

The extraordinary deficiency of models in the Nairobi district must doubtless play a part in promoting the great variability of subspecies *polytrophus*. But, for three reasons, I hesitate to ascribe it wholly to this cause. First, the frequency of models required to maintain mimetic stability is apparently much less in the Kakindu district than at Entebbe. However, it is at least suggestive that, in addition to the specimens here tabulated, Carpenter obtained 2 intermediates between *planemoides* and *trophonissa* (p. 440) in his collection of 27 * females of *P. dardanus* from the former locality. Secondly, the proportion of imperfect to fully developed mimics is higher in *trophonius* than in any other of the *polytrophus* forms except *salaami* (p. 443), while its model is not scarce (though there is evidence that the mimic is proportionately too common). Thirdly, there is no correlation between the amount of variability and the presence or absence of the appropriate models. It thus seems possible that *P. dardanus* is subject to less severe selection in the mountainous districts of Kenya Colony and Tanganyika Territory than elsewhere : perhaps the enemies which prey on it are less numerous. Such a situation, combined with the rarity of the models, might well be responsible for the great variability of the *polytrophus* race.

The various "*proto-salaami*" forms are a characteristic feature of this subspecies. Owing to the rarity of any appropriate models in the district it inhabits, and their own great variability, they cannot be regarded as mimetic. *dorippoides* was, however, named on the assumption that it copies the form

* This total is reached by the addition also of 1 *trophonissa* (p. 440), a form omitted from the present comparison for the reason already given.

*dorippus* Klug, of *Danaus chrysippus*. Now it is a striking fact that this modification of *chrysippus* is common within the range of subspecies *polytrophus*, but is absent on the west coast and very rare in South Africa, where no form of *dardanus* resembling it has ever been found. But it seems doubtful to me if *dorippoides* is really mimetic. It appears rather to represent the natural end-product of the gradual reduction in black pigment which frequently occurs in "*proto-salaami*" (pl. 3). The more extreme forms become progressively rare, and *dorippoides* itself is found least often of all. If, however, it were in reality an effective mimic, it should be commoner than the intermediates which lead to it.

The form *carpenteri* can be accurately matched by specimens of "*proto-salaami*" in which little black pigment is present. This name should, however, only be used for such individuals when occurring in the transitional race, in which it was originally described. For it seems undesirable to give a separate name to a particular stage in a continuous series.

## 5. Suggestions for Future Research.

It is highly desirable that experiments with marked females should be undertaken in a variety of species, especially in the tropics, to ascertain the frequency of multiple pairings. Forced matings (p. 456) with more than one male should also determine how often they give rise to broods of mixed paternity. Until these investigations have been carried out, all genetic results obtained by a study of females fertilised in nature are open to suspicion: whether or not the error involved is likely to be grave in some species and negligible in others, is not known. It will, however, be possible to estimate its magnitude in *P. dardanus* from the data tabulated in this paper, once the relations of the various forms have been established by controlled matings.

No further useful purpose can be served by breeding from captured females of this species. Such small additional results as could thus be achieved would be incommensurate with the time and labour involved. It is often an extremely difficult matter to induce butterflies to pair in captivity by ordinary means; but since Swynnerton has shown that forced matings are quite successful in *P. dardanus* (p. 456), accurate results are within the reach of all workers who have the opportunity of breeding it. Naturally it would often be very desirable to raise more than one generation in captivity, as has already been done on one or two occasions. But it is not essential to do this in order to solve many of the genetic problems awaiting investigation. Important information could be obtained by anyone who would breed a number of families from females of different forms, in such circumstances that multiple paternity could be excluded. For this purpose it is only necessary to collect wild larvae, separate the male and female pupae,* pair the imagines as required, and rear and record the resulting families. It should first be discovered if a single male can be made to pair with more than one female. If this is possible, it would be an advantage to mate *the same male* with females of different forms; a proceeding

* The sex of the future butterfly can be ascertained by examining the pupal wing-cases with transmitted light, from about the fourth day, if development is proceeding normally. It is then seen that though the space for the tail is present in both sexes, it is unoccupied by tissue in the females (Poulton, 1924*b*, editor's note, p. 12). Further, shortly before emergence the colour of the wings can be seen through the pupal covering, when the males are easily separable. (The sex of the pupa can, of course, be determined at any stage by examining the terminal segments on the ventral side. This would, however, necessitate detaching it from its support.)

which would greatly simplify the genetic analysis. Such work could, of course be undertaken in any of the races in which polymorphic females occur. It would, however, be more difficult in *d. dardanus* and *tibullus*, as the forms in a minority are so rare in these subspecies, while the use of subspecies *polytrophus* would introduce numerous complexities: the subspecies *cenea* seems especially suitable for preliminary study. Half as much work as has already been done would, if conducted on these lines, have gone far to elucidating the genetics of this species.

I regard the discovery by Mr. C. F. M. Swynnerton (1919) that it is possible to force *P. dardanus* (and, presumably, many other species) to pair in captivity, as one of great value. It seems but little known to entomologists, and it is a pleasure to draw attention to it here. For the benefit of those who have not the opportunity of referring to the original, I quote his own words: "Pairing now offers little difficulty. I have made it compulsory. The genitalia are brought into the correct juxtaposition, very slight pressure is exercised on the sides of the two abdomens with finger and thumb of each hand and, as soon as the male is seen (by abdominal movements) to take on, he is allowed to hang, and both are placed in a box, better dark. Some males refuse. The pairings of which I am now seeing the results [nos. 119–124, p. 462] were obtained in this way. The only infertile pairings were obtained with [subspecies] *cenea* males that I had had to keep some weeks to await the emergence of a *hippocoon* family."

Once the relationship of the chief forms has been established, work on a number of important lines will become possible. Some of these may briefly be indicated.

The theory of dominance-modification developed by Fisher (1931) may justly be regarded as one of the most important advances which have so far been made in the study of evolutionary genetics. This author was the first to recognise that dominance is a product of selection. He has furthermore developed the concept that this agency operates upon the gene-complex, modifying the response of the organism to the particular factor in question, which itself remains unchanged. When any gene is rare, it will exist almost wholly in the heterozygous state. If disadvantageous, those individuals will be favoured whose gene-complex interacts to bring out its effects to the least degree: the converse will be true for beneficial factors. In this way the tendency for characters to become respectively dominant or recessive is spread through the species, while the existence of recurrent mutation allows it repeated experience even of those genes which are regularly eliminated.

Fisher (1930) has pointed out that this process will be particularly rapid in polymorphic forms, in which the heterozygotes are so much commoner than in normal circumstances. Consequently it is conceivable that when the frequencies of a common and a rare form are reversed in different districts, their dominance relationships may also change. Fisher has further stressed the fact that the behaviour of genes when introduced into races unaccustomed to them should prove a crucial test of the present theory. For the dominance or recessiveness of a character should fail when the factor controlling it is immersed in a gene-complex which has had no opportunity of being adjusted to it. Not so if the dominance were due to a change in the factor itself, as it would be by the selection of a different member of the same multiple-allelomorph series. It is therefore a fact of great importance that such failures in dominance have actually been demonstrated (Harland, 1933; Fisher, 1935).

From the account so far given in this paper, it will be apparent that *P. dardanus* provides exceptionally good material for a study of such phenomena. At Durban, the *cenea* form is about nine times as common as *hippocoonides*, while at Dar-es-Salaam *hippocoonides* is perhaps twenty times as common as *cenea*. Are their dominance relations in any way affected? Such evidence as is available suggests that they are not,* but one cannot yet be certain. It will be much more important, however, to learn the result of crossing the *cenea* form of female (preferably of the transitional race) with west-coast males, belonging to the race *dardanus dardanus*, in which it either does not exist or is excessively rare.

A special effort should be made to study the genetics of *P. dardanus antinorii*, and to determine the relation of the mimetic to the male-like females. In addition, crosses between this and the other subspecies would show if the tailed condition of the female differs from the tailless by one or many factors, and should demonstrate whether or not the tailed mimics are produced by the same gene as the corresponding tailless forms: *niavioides* and *hippocoon*, *ruspinae* and *trophonissa*, even *wienholti* and *niobe*, may perhaps prove to be manifestations of identical factors in different internal environments.

The increasing facilities for sending material by air should make work involving racial crosses quite practicable. However, it has already been possible to send the pupae of this species safely by post for considerable distances in Africa. Thus a consignment of pupae of the *cenea* race from Durban arrived safely at Chirinda in south-eastern Rhodesia, when Swynnerton succeeded in crossing the resulting imagines with the local subspecies *tibullus* (p. 446).

Finally, it will be important to study the mechanism by which the polymorphism is maintained in *P. dardanus*. The existence of this phenomenon must always involve a selective advantage so balanced against some disadvantageous condition that, as the proportion of the favoured form rises, the benefit it receives wanes and is finally reversed (*see* Fisher, 1927, and Ford, 1934). The mimicry of a more by a less well-protected species should alone be sufficient to preserve such an equilibrium in certain circumstances. It will also arise automatically if the more favoured form is dominant, and the heterozygote possesses some physiological advantage over the homozygote, being, for example, more fertile. Thus Fisher (1930) studied the data obtained by Nabours (1925) in his work on *Apotettix* (Orthoptera), and found a significant deficit of the homozygous dominant class.

In mimetic butterflies it seems that these two methods are sometimes combined. Fryer (1913) encountered numerous sterile unions in his breeding experiments with *Papilio polytes* L., and Fisher (1927) pointed out that one of the simplest explanations of such an occurrence is a greater fertility of the heterozygotes as compared with the homozygotes. I have elsewhere shown that there is ground for suspecting a deficiency of the homozygous dominants in segregation between the female forms *misippus* and *inaria* of *Hypolimnas misippus* (Carpenter and Ford, 1933 : 120). It will be extremely interesting to learn if a similar mechanism operates in *P. dardanus* and, if so, whether it affects all, or some only, of the forms. It will be revealed by an approach towards a 2 : 1 ratio in those families in which a ratio of 3 : 1 is expected. It

* Except for the possible indication provided by no. 11. But the abnormal proportions in this family are much more probably due to multiple matings (p. 451). For the crosses between subsp. *cenea* and *tibullus* strongly suggest that *hippocoonides* is recessive to the *cenea* form in both.

is probable that the extreme condition, with one of the homozygous classes absent, is rather often attained in this type of control. In these circumstances, it is not correct to describe the heterozygous phenotype as dominant.

## 6. Tables of Bred Families.

The families are provided with consecutive numbers to facilitate reference. Only female offspring are included, the males being monomorphic.

*Race :—d. dardanus.*

| | Parent :—*hippocoon.* | | | | | | |
|---|---|---|---|---|---|---|---|
| No. | *cenea* | *trophonissa* | *dionysos* | *hippocoon* | Locality | Bred by | Recorded |
| 1 | – | – | – | 14 | Lagos | Lamborn | 1913, *a* |
| 2 | – | – | – | 13 | ,, | ,, | ,, |
| 3 | – | – | – | 10 | ,, | ,, | ,, |
| 4 | – | – | – | 14 | ,, | ,, | ,, , *b* |
| 5 | – | – | – | 7 | ,, | ,, | ,, |
| 6 | – | – | – | 6 | ,, | ,, | ,, |
| 7 | – | – | 8 | 9 | S. Nigeria | ,, | 1915 |

*Race :—dardanus (transitional).*

| | Parent :—*planemoides.* | | | | | | |
|---|---|---|---|---|---|---|---|
| No. | *cenea* | *trophonissa* | *planemoides* | *hippocoon* | Locality | Bred by | Recorded |
| 8 | 2 | – | 2 | 2 | Jinja dist. | Fountaine | – |
| 9 | – | – | 3 | 7 | V. Nyanza | Carpenter | 1913 *a*, *b* |
| | Parent :—*carpenteri.* | | | | | | |
| 10 | – | 1 | 1 | – | V. Nyanza | Carpenter | 1916 |

*Race :—dardanus tibullus.*

| | Parent :—*cenea* (*y*). | | | | | | |
|---|---|---|---|---|---|---|---|
| No. | *cenea* | *trophonius* | *natalica* | *hippocoonides* | Locality | Bred by | Recorded |
| 11 | 4 (*y*) | – | – | 13 | Chirinda | Swynnerton | 1915 |
| 12 | 2 (*y*) | – | – | 1 | ,, | ,, | ,, |
| | Parent :—*trophonius.* | | | | | | |
| 13 | – | 4 | – | 3 | Chirinda | Swynnerton | 1915 |
| | Parent :—*natalica.* | | | | | | |
| 14 | – | – | 5 | 3 | Chirinda | Swynnerton | 1915 |

*Race :—dardanus tibullus* (contd.).

| | Parent :—*hippocoonides.* | | | | | | |
|---|---|---|---|---|---|---|---|
| No. | *cenea* | *trophonius* | *natalica* | *hippocoonides* | Locality | Bred by | Recorded |
| 15 | – | – | – | "all" | Tanga | Lamborn | Poulton, 1924 *b* |
| 16 | – | – | – | 2 | ,, | ,, | 1917 |
| 17 | – | – | – | 16 | S.E. Rhodesia | Swynnerton | – |
| 18 | – | – | – | 9 | Chirinda | ,, | 1915 |
| 19 | – | – | – | 7 | ,, | ,, | ,, |
| 20 | – | – | – | 16 | ,, | ,, | ,, |
| 21– | – | – | – | 1, 3, 5 | ,, | ,, | ,, |
| 35 | | | | 3, 5, 5 | ,, | ,, | ,, |
| | | | | 5, 2, 4 | ,, | ,, | ,, |
| | | | | 4, 6, 3 | ,, | ,, | ,, |
| | | | | 8, 10, 12 | ,, | ,, | ,, |
| 36 | – | – | – | 1 | E. Rhodesia | ,, | – |

*Race :—dardanus cenea.*

| | Parent :—*cenea.* (See also nos. 119 and 122.) | | | | | | |
|---|---|---|---|---|---|---|---|
| No. | *cenea* | *trophonius* | *leighi* | *hippocoonides* | Locality | Bred by | Recorded |
| *i* 37 | 16 (*s*) | – | – | 1 | Durban | Leigh | Poulton, 1908 |
| 38 | 24 | – | – | 3 | ,, | ,, | ,, ,, |
| *y* 39 | 3 (2 *y*, 1 *w*) | – | 2 | 1 | ,, | ,, | – |
| 40 | 21 (16 *i*, 5 *w*) | – | – | 2 | ,, | ,, | – |
| | Parent :—*trophonius.* | | | | | | |
| 41 | 6 (*y*) | 1 | – | – | Durban | Leigh | Poulton, 1906 |
| 42 | 2 (1 *y*, 1 ?) | – | – | – | ,, | ,, | ,, 1908 |
| 43 | 22 (14 *y*, 7 *w*) | 4 | 2 | 2 | ,, | ,, | ,, 1912 |
| 44 | 9 | 4 | 1 | 2 | ,, | ,, | ,, 1913 |
| 45 | 7 (*y*) | – | – | 11 | ,, | ,, | – |
| 46 | 12 | 1 | – | 5 | ,, | ,, | – |
| 47 | 2 | 22 or 23 | – | – | ,, | Fountaine | 1913 (*see* p. 451) |
| | Parent :—*hippocoonides.* | | | | | | |
| 48 | 8 (4 *y*, 4 *w*) | 3 | – | 3 | Durban | Leigh | Poulton, 1908 |
| 49 | 13 (6 *y*, 7 *w*) | – | – | – | ,, | ,, | ,, ,, |
| 50 | 14 | 2 | – | 4 | ,, | ,, | – |
| 51 | 17 | 8 | – | 11 | ,, | ,, | Talbot, 1917 |
| 52 | 13 (9 *y*, 4 *w*) | – | – | 2 | ,, | ,, | – |
| | Parent :—*leighi.* | | | | | | |
| 53 | – | – | – | 1 | Durban | Leigh | – |

*Race :—dardanus polytrophus.*

| No. | *cenea* n | *cenea* p | "*proto-trophonius*" | "*proto-salaami*" n | "*proto-salaami*" p | *planemoides* n | *planemoides* p | *swynnertoni* | *hippocoonides* n | *hippocoonides* p | Bred by | Remarks |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Locality for all broods :—Nairobi. None previously recorded, except no. 112 (Poulton, 1924*a*) | | | | | | | | | | | |
| | Parent :—*cenea*. | | | | | | | | | | | |
| 54 | 3 | – | – | – | – | – | – | – | 3 | – | Rogers | |
| 55 | – | – | – | – | – | – | – | – | 1 | – | ,, | |
| 56 | 12 | – | – | – | – | – | – | – | 2 | – | van Someren | |
| 57 | 4 | – | – | – | – | – | – | – | 4 | – | ,, | |
| 58 | 2 | – | – | – | – | – | – | – | – | – | ,, | |
| 59 | 1 | – | – | – | – | – | – | – | 1 | – | ,, | |
| 60 | 9 | – | – | – | – | – | – | – | 4 | – | ,, | |
| 61 | 18 | – | – | – | – | – | – | – | – | – | ,, | |
| 62 | 6 | – | – | – | 2 | – | – | – | 1 | – | ,, | |
| 63 | 6 | – | – | – | – | – | – | – | 1 | – | ,, | |
| 64 | – | 1 | 4* | – | – | – | – | – | – | – | ,, | |
| 65 | 13 | 7 | – | – | – | – | – | – | – | – | ,, | |
| 66 | 7 | 1 | – | – | – | – | – | – | – | – | ,, | F1 of 65 |
| 67 | 2 | 1 | – | – | – | – | – | – | 2 | – | ,, | |
| 68 | 7 | – | – | – | – | – | – | – | 2 | – | ,, | |
| 69 | – | 2 | – | – | – | – | – | – | – | – | ,, (?) | |
| 70 | – | 24 | – | – | 1 | – | – | – | 4 | – | ,, | |
| 71 | – | – | 7 | – | – | – | – | – | – | – | ,, | |
| 72 | 1 | – | 2 | – | – | – | – | – | 1 | – | ,, | |
| | Parent :—"*proto-cenea*." | | | | | | | | | | | |
| 73 | – | 1 | – | – | – | – | – | – | 5 | 6 | ,, | |
| 74 | – | 3 | – | – | – | – | – | – | 6 | – | ,, | |
| 75 | 5 | 3 | – | – | – | – | – | – | – | – | ,, | |
| 76 | 2 | 1 | – | – | – | – | – | – | 1 | – | ,, | |
| 77 | 9 | 6 | – | – | – | – | – | – | 1 | – | ,, | |
| 78 | 5 | 4 | – | – | – | – | – | – | 5 | – | ,, | |
| 79 | 9 | – | – | – | – | – | – | – | 1 | – | ,, | |
| 80 | – | 4 | – | – | 7 | – | – | – | 4 | – | ,, | |
| 81 | 1 | 5 | – | – | – | – | – | – | 7 | – | ,, | |
| 82 | – | 13 | – | – | 1 | – | – | – | 4 | – | ,, | |
| 83 | – | 4 | – | – | – | – | – | – | – | – | ,, | F1 of 65 |
| 84 | – | 5 | 8 | – | – | – | – | – | – | – | ,, | ,, ,, ,, |
| | Parent :—"*proto-trophonius*." | | | | | | | | | | | |
| 85 | 13 | 5 | 12 | – | – | – | – | – | 12 | – | ,, | pl. 2, fig. 4 |
| 86 | 1 | 7 | 10 | – | 27† | – | – | – | 19 | – | ,, | (See note for figs.) |
| 87 | 4 | – | 6 | – | – | – | – | – | 5 | – | ,, | |
| 88 | – | – | 6 | – | – | – | – | – | 5 | – | ,, | pl. 2, fig. 3 |

* Of these, 3 are intermediate between "*proto-trophonius*" and *cenea*.

† Series from *poultoni* to *dorippoides*. (Insects from this family are figured on pl. 2, fig. 2, pl. 3, figs. 1–8.)

*Race :—dardanus polytrophus* (contd.).

| No. | *cenea* n | *cenea* p | "*proto-trophonius*" | "*proto-salaami*" n | "*proto-salaami*" p | *planemoides* n | *planemoides* p | *swynnertoni* | *hippocoonides* n | *hippocoonides* p | Bred by | Remarks |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Parent :—"*proto-salaami.*" | | | | | | | | | | | |
| *n* 89 | 1 | – | – | – | 1 | – | – | – | 1 | – | van Someren | |
| *p* 90 | – | – | – | – | 6 | – | – | – | 7 | – | ,, | |
| *p* 91 | 6 | – | – | – | 7 | – | – | – | – | – | ,, | |
| 92* | – | – | – | – | 18 | – | – | – | – | – | ,, | trans. to *mixtus* |
| *n* 93 | 2 | – | – | – | 8 | – | – | – | 13 | – | ,, | |
| *p* 94 | – | – | – | – | 2 | – | – | – | 2 | – | ,, | F1 of 93 |
| *p* 95 | – | – | – | – | 2† | – | – | – | 1 | – | ,, | |
| *n* 96 | – | – | 2 | 5 | – | – | – | – | 1 | – | ,, | |
| *p* 97 | – | – | – | – | 2 | – | – | – | 2 | – | ,, | |
| *n* 98 | – | – | 3 | – | 4 | – | – | – | – | – | Rogers | pl. 2, fig. 7 |
| | Parent :—*planemoides.* | | | | | | | | | | | |
| 99 | 2 | – | 1 | – | – | – | 2 | 4 | 11 | – | van Someren | |
| | Parent :—"*proto-planemoides.*" | | | | | | | | | | | |
| 100 | 5 | 1 | – | – | – | – | 2 | – | 9 | 1 | ? | |
| | Parent :—*swynnertoni* (abnormal, F.W. as in *poultoni*) [see pl. 4, fig. 1]. | | | | | | | | | | | |
| 101 | – | 1 | 2 | – | 2 | 1 | 1 | – | – | – | Rogers | ‡ 1 *leighi* |
| | Parent :—*hippocoonides.* | | | | | | | | | | | |
| 102 | – | – | – | – | – | – | – | – | 18 | – | van Someren | |
| 103 | – | 1 | 2 | – | – | – | – | – | 1 | 3 | ,, | |
| 104 | – | – | – | – | – | – | – | – | 6 | – | ,, | |
| 105 | 7 | 1 | – | – | – | – | – | – | – | – | ,, | |
| 106 | – | – | – | – | – | – | – | – | 8 | – | ,, | |
| 107 | – | – | – | – | – | – | – | – | 20 | 2 | ,, | |
| 108 | – | 1 | – | – | – | – | – | – | 5 | – | ,, | |
| 109 | 2 | – | – | – | – | – | – | – | 8 | – | ,, | |
| 110 | 2 | – | – | – | – | – | – | – | 5 | – | ,, | |
| 111 | 1 | 4 | – | – | – | – | – | – | 7 | – | ,, | |
| 112 | – | 5 | – | – | – | – | – | – | 3 | – | ,, | |
| 113 | 1 | – | – | – | – | – | – | – | 2 | – | ,, (?) | |
| 114 | 3 | – | – | – | – | – | – | – | 4 | – | ,, | |
| 115 | 1 | – | – | – | – | – | – | – | – | – | Rogers | intersex |
| | Parent :—"*proto-hippocoonides.*" | | | | | | | | | | | |
| 116 | 4§ | 1 | – | – | – | – | – | – | 2 | 3 | van Someren | |
| | Parent :—intermediate, *cenea* and "*proto-trophonius*" (van Someren) | | | | | | | | | | | |
| 117 | 2 | 1 | 1 | 2 like parent, 1 int. "*p. cenea*" and "*p. hippocoonides.*" | | | | | | | | pl. 2, figs. 5 and 6 |
| | Parent :—intermediate, *natalica* and "*proto-cenea*" (van Someren). | | | | | | | | | | | |
| 118 | – | 11 | – | 7 like parent. | | | | | | | | |

* Parent intermediate between *poultoni* and normal "*proto-salaami.*" The 18 offspring form a series from one extreme to the other.

† Intermediates between *poultoni* and "*proto-salaami.*"

‡ This family also contained one intersex, but the ♀ form represented in it is doubtful. (The parent of this family, and members of the offspring, are figured on pl. 4, figs. 1–10.)

§ Of these, 1 is intermediate between *cenea* and "*proto-hippocoonides.*"

Races *cenea* and *tibullus* interbred.

As described on p. 446, Swynnerton (1919), working at Chirinda, obtained race *cenea* from Natal, supplied by Mr. E. E. Platt. This he crossed with the local *tibullus* as follows :—

| | Parents :—*cenea* ♂ and ♀ (Natal). | | |
|---|---|---|---|
| No. | *cenea* | *hippocoonides* | |
| 119 | "all" | – | One of these was interbred with a *tibullus* ♂ to give :— |
| 120 | 1* | – | |
| | Parents :—*cenea* ♀ (F1 from Natal imagines interbred) X *tibullus* ♂. | | |
| 121 | 10 | – | |
| | Parents :—*cenea* ♂ and ♀ (Natal). | | |
| 122 | some | some | (numbers not given). |
| | Parents :—*cenea* ♀ (from 122) X *tibullus* ♂. | | |
| 123 | 2* | 3 | |
| | Parents :—*hippocoonides* ♀ (from 122) X *tibullus* ♂. | | |
| 124 | – | 6 | |

* = "incomplete" *cenea*, see p. 451. Some of family no. 122 were "incomplete *cenea*"; numbers not given.

All the families here summarised are in the Hope Department of Entomology at Oxford, with the exception of the following :—nos. 40, 46, and 52 are in the British Museum (Natural History). No. 38 has been partly dispersed among private collections, while the remainder of it is at Oxford. Nos. 8 and 47 are in private collections. No. 51 was destroyed. No. 50 was also partly destroyed, but the remainder of it is at the British Museum. The whereabouts of nos. 16, 15, 72, 87, 88, 97, 113–115, 119–124 is unknown to me. Details of the first two and the last six have been obtained from the published accounts of them, and of the others from information supplied by Sir Edward Poulton.

I have myself examined every family here recorded, except nos. 8, 15, 16, 47, 51, 72, 87, 88, 97, 113–115, 119–124.

The yellow-, intermediate-, and white-spotted *cenea* forms (p. 440) are distinguished by the letter *y*, *i*, or *w* after the name. If all parents are of one type, the distinguishing letter is placed in the heading; where they are not, it is placed in front of the particular brood-number in question. Among the offspring, the total number of the *cenea* form is given first, then the numbers of the yellow- and white-spotted forms. An *s* indicates that they can be arranged as a graded series from the one to the other. I do not know the proportion of these forms in the families I have not myself seen; furthermore, it is not possible to separate them in worn specimens. Hence their numbers do not always add up to the *cenea* total, as some may be damaged or faded. For the same reason, the parents are often without any distinguishing sign. I have

not separated the yellow- and white-spotted *cenea* in the race *polytrophus*. In view of its great variability, the attempt seemed difficult and nearly useless.

The *cenea*, *planemoides*, and *hippocoon* forms of *polytrophus* are sub-divided under the headings *n* and *p*. These stand for the normal and imperfectly developed mimics (i.e. "*proto-cenea*," "*proto-planemoides*," "*proto-hippocoon*"). The distinction between *cenea* and "*proto-cenea*" cannot always be directly determined. I have, however, tested all doubtful specimens by examination with ultra-violet light (p. 442), and I believe that their classification may safely be accepted.

Under "*proto-salaami*," *p* indicates *poultoni* and *n* the normal *salaami*-like form. The parents are also distinguished by these letters.

A reference is given to each family that has previously been recorded. It is to be understood that the breeder is also the author of the record, unless the contrary be stated.

## 7. Summary.

1. *Papilio dardanus* forms a number of subspecies, fertile with one another, within most of which the females are polymorphic. It consequently provides quite exceptional opportunities for genetic research.

2. The distribution of the various races is discussed, the different forms of female occurring in each are described and estimates given of their relative frequencies.

3. The numerous female forms are determined genetically by sex-controlled autosomal genes. Many, but not all, are uni-factorial in inheritance.

4. *dionysos* is a heterozygous form. There is, at present, no justification for regarding it as a dominant.

5. *trophonissa* is probably converted into *niobe* by a single "modifying factor."

6. *natalica* is probably due to a heterozygous modification of *hippocoonides*.

7. The *cenea* form is dominant both to *hippocoonides* and to *trophonius*. A single factor probably converts *hippocoonides* (but not *cenea*) into *trophonius*. It is, however, uncertain if the latter is dominant or recessive to *hippocoonides*.

8. "*proto-salaami*" is dominant to *hippocoonides*, and *poultoni* is a genotypic modification of it.

9. The genetic relationships of a number of other female forms are discussed.

10. Evidence is brought forward to show that *P. dardanus* often pairs more than once in nature, and produces broods of mixed paternity, as many other butterflies seem to do.

11. The frequency of models relative to mimics is studied in one of the races with fully developed mimicry, and in *polytrophus*. It is concluded that the great variability of the latter subspecies is partly, but not wholly, due to a proved deficit of models in the region it inhabits.

12. It is suggested that certain precautions should be adopted in future research on this butterfly, and the most important problems awaiting investigation are discussed.

(*a*) The frequency of multiple pairings in nature must be ascertained.

(*b*) It will be of but little further use to breed from captured females of *P. dardanus*.

(*c*) All future work should be conducted on females bred in captivity and known to be mated with a single male only.

(*d*) The same male should, if possible, be mated to two or more virgin females of different forms.

(*e*) Attention is drawn to Mr. C. F. M. Swynnerton's discovery that this species can easily be forced to pair in captivity. This makes it quite possible to conduct work on the lines suggested above.

(*f*) The theory of dominance-modification can be studied to great advantage in *P. dardanus*, by crossing the different subspecies. In this way, the genetic behaviour of given forms of female can be investigated when crossed with races in which they are rare or absent.

(*g*) A special effort should be made to determine the relation of the mimetic to the male-like females, and of the tailed to the tailless mimics.

(*h*) It should be established if the homozygous dominant class is rare or absent when any of the forms of this species segregate.

13. As far as can be ascertained, all previous breeding experiments on *P. dardanus* are tabulated with full details.

14. A new female form (*poultoni*) of subsp. *polytrophus* is described.

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## 9. Appendix.

**Papilio dardanus** ♀-form. **poultoni** form. n.

Pl. 3, figs. 1 and 2.

This is one of the numerous modifications of *salaami* Suf., in which the spot in area 8 of the forewing (sometimes reduplicated in area 9) is yellowish or even white, as is a small patch at the proximal end of the cell-spot. All the other lighter areas in the fore- and hind-wings are reddish-brown, while the black markings have approximately the same distribution as in *trophonius*. The sub-apical bar may, however, be enlarged until it fuses with the spot in the cell. The present form is distinguished by a black wedge-shaped bar extending outwards from the basal area of the fore-wings part of the way across the large brown patch on the hind margin. This wedge lies in area 1*b* but, when enlarged, may extend beyond it in either direction. It is often more pronounced than in the specimen figured.

The form constitutes an important element in the *polytrophus* population, but it is also found occasionally in subspecies *tibullus*. Thus Dr. Wiggins caught a specimen 10 miles inland from Mombasa, and Canon Rogers obtained one in the Dabida Mountains, British East Africa.

This is an easily recognised variety, and the tendency to produce it is inherited (p. 450). Furthermore, intermediates between it and the other forms of "*proto-salaami*" are very infrequent. For these reasons it has become useful to separate it, and I have much pleasure in associating it with the name of Sir Edward Poulton, whose work on *P. dardanus* has been of outstanding importance in the analysis of mimicry.

*Type*.—A female in the Hope Collection, Oxford, bred by Dr. van Someren on 17 May, 1923, with five others (paratypes) from a female of the same form caught at Nairobi, Kenya Colony, 3 March, 1923. (The family also included seven *hippocoonides*; no. 90, p. 461.)

## Explanation of Plates 1–4.

### Plate 1.

*P. dardanus antinorii* Oberth., f. *wienholti* Poulton (type). W. Abyssinia: Gore, 14.xii.1926 (*A. W. Hodson*). This unique specimen has not previously been figured.

### Plate 2.

*P. dardanus polytrophus* R. & J. ("*proto-trophonius*" and its modifications; all are from Nairobi).

Figs. 1 & 3: *lamborni* Poulton, the latter being the more usual form.

2; 4–8: modifications of *lamborni* (fig. 6 is intermediate between *lamborni* and *cenea*).

fig. 1: captured by Canon Rogers, 22.x.1922.
2: bred by Dr. van Someren [from no. 86, p. 460].
3: ,, ,, ,, ,, ,, [ ,, no. 88, p. 460].
4: ,, ,, ,, ,, ,, [ ,, no. 85, p. 460].
figs. 5 & 6: ,, ,, ,, ,, ,, [ ,, no. 117, p. 461].
fig. 7: ,, ,, Canon Rogers [ ,, no. 98, p. 461].
8: captured by Canon Rogers, 6.xi.1922.

### Plate 3.

*P. dardanus polytrophus* ("*proto-salaami*" and its modifications, bred by Dr. van Someren at Nairobi). [Part of family no. 86, p. 460.]

Figs. 1 & 2: *poultoni* form. n.
Fig. 4: "*proto-salaami*."
Figs. 3 & 5: forms slightly transitional towards *poultoni*.
6 & 7: forms transitional towards *dorippoides*.
Fig. 8: *dorippoides* Trim.

### Plate 4.

*P. dardanus polytrophus*. [Part of family no. 101, p. 461, bred by Canon Rogers at Nairobi.] (Fig. 1 = ♀ parent, figs. 2–10 = offspring.)

Fig. 1: "*proto-planemoides*" aberrant, F.W. as in *poultoni* (*swynnertoni* form, but hind-wings worn nearly white).
2: *planemoides*.
3: "*proto-planemoides*."
4: *leighi* (a somewhat aberrant form).
Figs. 5 & 7: *poultoni*.
6 & 8: "*proto-trophonius*."
Fig. 9: A sex-intergrade, perhaps an intersex.
10: "*proto-cenea*."

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